Spatio-temporal changes of terrestrial isopod assemblages (Isopoda: Oniscidea) in a fen undergoing succession

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ABSTRACT

Peatlands in the Western Balkans are becoming rapidly reduced due to vegetation succession, further enhanced by climate change and abandonment of traditional land management practices. Currently, the peatlands of this region act as habitat islands embedded mainly in a forest landscape matrix. This allows them to host more forest and generalist species of animals and plants than would be expected from such ecosystem. We were interested in testing if a taxon, unspecialized for such extreme habitats, can maintain stable populations in a peatland, and how environmental fluctuations affect its spatio-temporal distributions along a successional gradient. Terrestrial isopods were sampled in four habitat types: a fen, two successional habitats and a beech forest, with pitfall traps during two consecutive years. In total, 1069 individuals belonging to five species were recorded. Activity density increased more than four-fold along the successional gradient, from the fen to an older and more complex successional habitat. This pattern was governed by an increase in the structural complexity of the habitat, where succession habitats supported more favourable shelter sites for terrestrial isopods. Soil moisture decreased over 30% along the successional gradient. Additionally, the older successional habitat was more nutrient rich than the fen, providing higher substrate quality for decomposers and enabling the survival of forest species. The fen was inhabited by a single species, *Ligidium germanicum*, while other species were extremely rare. Its seasonal activity started in the spring, reaching the maximum in June and decreasing at the end of summer. Spatial changes in isopod assemblages along the successional gradient imply that the groundwater level in the fen was sufficiently high to supress the invasion of forest species into the fen. Colonisation of the fen by terrestrial isopods will likely progress as environmental conditions become more suitable by progressive vegetation succession and climate change.

1. Introduction

Communities of soil macroinvertebrates differ in composition and structure along the gradient of physicochemical soil properties, such as soil structure, texture, moisture and pH (Savin et al., 2007; Decaëns, 2010). In acidic soils, bacterial and macrofaunal diversity is reduced in comparison to neutral soils (Scheu and Poser, 1996; Jeffery et al., 2010). The abundance and diversity of macroinvertebrates further decreases with increasing soil moisture (Silvan et al., 2000). Thus, changes in soil physicochemical properties influence spatial distribution of soil biota and its population dynamics (Warburg, 1987; Monroy et al., 2006; Savin et al., 2007). In temperate ecosystems, some of these changes are caused by seasonal variations that affect animal life cycles and population densities (Doblas-Miranda et al., 2007; Brigić et al., 2016).

Terrestrial isopods are an ecologically diverse group of soil invertebrates that inhabit a wide range of terrestrial biomes (Hornung, 2011). They feed on different food sources, with higher preference for dicotyledonous plants than for bryophytes or monocotyledonous plants (Rushton and Hasall, 1983). Thus, they play an important role in nutrient cycling through the decomposition of litter and stimulation of fungal and bacterial activity (Loureiro et al., 2006). Due to their
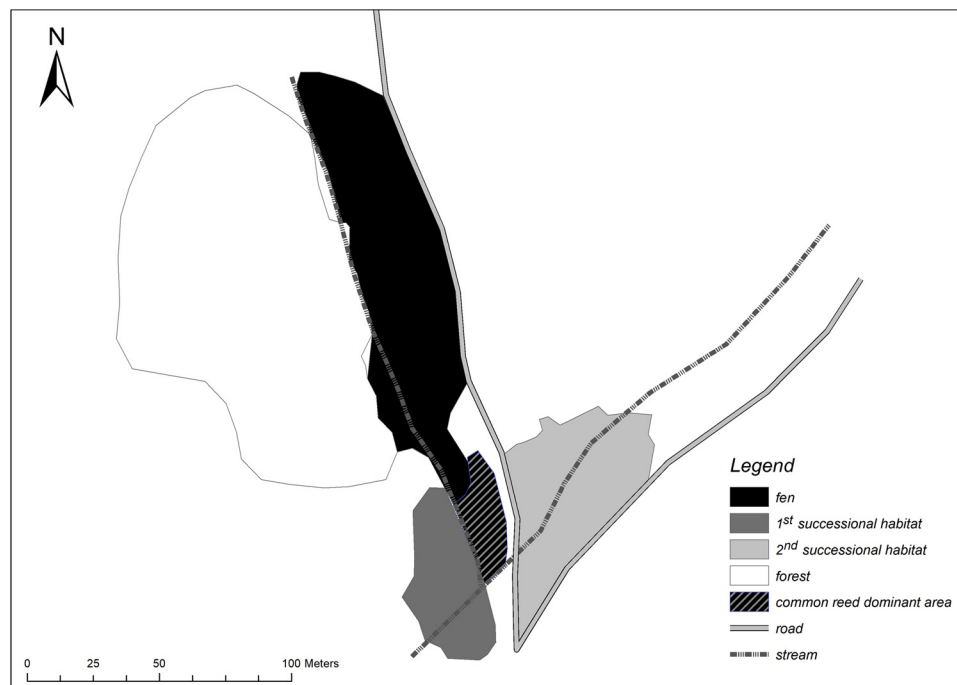

Fig. 1. Vegetation map of the Jarak fen (Croatia).

sensitivity to environmental changes, particularly soil moisture, they can be used as bioindicators (Wolters and Ekschmitt, 1997; Paoletti and Hassall, 1999). Isopod species select micro-habitats as refuges or shelters depending on their moisture preferences and, to a certain extent, the concentration of sodium chloride and calcium carbonate salts in the soil (Warburg et al., 1984). Thus, their spatial distribution and epigeic activity are positively correlated with moisture (c.f in Tuf and Jeřábková, 2008), and varies by season (Zimmer and Brauckmann, 1997; Antonović et al., 2012).

The seasonality of terrestrial isopod distribution is governed by abiotic and biotic factors (Warburg, 1987; Hornung, 2011). Population density, as well as the beginning and duration of the breeding period, vary among species and within various populations of the same species (Warburg, 1987; Achouri and Charfi-Cheikhrouha, 2005). Differences in phenology are driven by seasonality, climatic conditions (Warburg et al., 1984; Zimmer and Brauckmann, 1997) and food quality (Zimmer and Topp, 2000). Environmental factors can influence population dynamics, e.g. high isopod abundance can be a result of high precipitation in the previous year (Warburg et al., 1984), while high air temperatures in early spring support the early beginning of reproduction in terrestrial isopods (Heath and Khazaeli, 1985).

Habitats experiencing vegetation succession commonly experience changes in nutrient availability, soil moisture and mineralization (Bautista-Cruz and del Castillo, 2005). Peatlands in the Western Balkans are an example of such habitats. Vegetation succession caused by climate change and abandonment of traditional management practices have caused rapid reduction in peatland size in this region (Topić and Stančić, 2006; Alegro and Topić, 2017). In general, vegetation succession alters not only the size of the peatland, but also the microclimate conditions. Peatlands overgrown by woody vegetation are dryer, have lower temperature fluctuations, and higher oxygen availability in the rhizosphere (Weltzin et al., 2003; McNamara et al., 2008). These altered conditions cause increase in species diversity and abundance of soil fauna (Silvan et al., 2000; Aleksandrowicz, 2002) and losses of peatland-specific species, enabling colonization of generalists or hygrophilous species, such as ants, carabid beetles and isopods (Bujan et al., 2015; Brigić et al., 2017a, b).

The objectives of this study were to test for spatial and temporal changes of terrestrial isopod assemblages in a fen (basophilic peatland) and the surrounding habitats. To do so, we first examined the differences in activity density and community composition between the fen, succession habitats, and the forest. This allowed us to test which habitats and which abiotic conditions are preferred by terrestrial isopods. We then explored the seasonal variation of isopod activity, as their activity density across seasons informs their life cycle (Zimmer and Brauckmann, 1997). Seasonal variation in activity density can reveal which habitats are the most important for reproduction and maintenance of stable populations of terrestrial isopods. This is the first study examining the seasonal dynamic of isopod assemblages in a basophilic peatland in the Western Balkans.

2. Material and methods

2.1. Study area

We sampled a terrestrial isopod community in the Jarak fen situated in the west-central Croatia, near the village Sošice (N 45°45′46.44″, E 15°22′1.2″), at an elevation of 690 m. The fen is part of the Žumberak–Samoborsko Gorje Nature Park. This region is characterized by a temperate climate with a mean annual temperature of 6.5 °C and mean annual precipitation of 1450 mm (Zaninović et al., 2008). Jarak fen is an alkaline fen, developed on dolomite bedrock (Pleničar et al., 1975; Pleničar and Premru, 1977). It is a nutrient poor, minerotrophic peatland nourished by ground water. Since the mid-20th century, the fen area has decreased from 2.5 ha to 1 ha, due to the abandonment of traditional land management practices, particularly livestock grazing and mowing (Šoštarić and Sedlar, 2008; Radić, personal communication). As a result, the vegetation composition and structure have changed due to the spread of *Phragmites australis* (Cav.) Trin. ex Steud), *Salix* sp. and *Populus tremula* L. (G). Four main habitats were selected to represent a succession gradient: the fen, the 1st successional habitat, the 2nd successional habitat and the forest (Fig. 1). These habitats differ in their vegetation composition, structure and pedological properties (e.g. soil moisture, soil pH and soil type; Table 1).

The fen is positioned in a gorge, near a small stream. It is developed on the rendzina soil (Kalinić et al., 1969; Mayer, 1976), belonging to

Table 1

Vegetation and soil properties measured in the fen, successional habitats and forest. Recorded values are presented as mean ± SD. Different letters indicate significant differences (p < 0.05). Legend: D - dicotyledonous, M - monocotyledonous plant species.

Vegetation and soil properties	Fen	1st successional habitat	2nd successional habitat	Forest	Kruskal-Wallis H test
Plant species richness (total)	42	49	91	10	
D : M ratio	27 : 15	38 : 8	75 : 14	8 : 2	
Soil mineral nitrogen availability (N-index)	3.81 ± 0.12b	5.55 ± 0.24b,c	6.04 ± 0.17a,c	5.02 ± 0.72b,c	18.25
Soil moisture (%)	82.1 ± 9.50a	54.20 ± 11.70c	52.50 ± 8.60b,c	56.80 ± 11.90b	30.13
Soil pH	7.01 ± 0.10b,c	7.42 ± 0.15a	7.31 ± 0.18b	5.64 ± 0.51c	32.22
Soil temperature (°C)	11.05 ± 6.00a	11.18 ± 6.62a	11.76 ± 6.22a	11.7 ± 4.74a	0.56

fibric soil type. The fen vegetation belongs to the *Eriophoro latifolio-Caricetum panicae* HT ex TRINAJSTIĆ association, with *Eriophorum latifolium* Hoppe dominating the site. Additionally, fen specific plant species *E. angustifolium* Honck. and four *Carex* spp. (*C. flacca* Schreb., *C. caryophyllea* Latourr., *C. hostiana* DC. and *C. paniculata* L.) were found in high abundance. *Phragmites australis* has successfully invaded one side of the fen (Fig. 1).

The 1st and 2nd successional habitats are located near mountain streams, and they grow on the luvisoil soil type (Kalinić et al., 1969; Mayer, 1976). The 1st successional habitat, covering an area of 0.15 ha, was dominated by *Salix cinerea* L., *P. australis* and *Petasites hybridus* (L.) P.Gaertn., B.Mey. & Schreb. These plants, particularly dicotyledonous *P. hybridus*, form dense stands surrounding the fen from the southern side. The 2nd successional habitat represents a young forest that is a mixture of *Salix* species, *P. tremula* and *Acer campestre* L. The herbaceous layer is composed of *P. hybridus*, *Eupatorium cannabinum* L., *Lysimachia vulgaris* L. and *Lythrum salicaria* L. It is spread on 0.26 ha. Specialized fen plants were sporadic or completely absent in the successional habitats.

The slope above the fen, with an inclination of 30-50°, is covered with a beech forest, with *Fagus sylvatica* L. dominating the tree layer (*Luzulo luzuloidi - Fagetum* Meusel, 1937 association). This forest is spread over 1 ha and experiences rapid erosion caused by the steep inclination and high precipitation. As a result, an acidophilous association with a poor herbaceous and a deep leaf litter layer is formed around the trees.

2.2. Sampling and identification

Terrestrial isopods were sampled using pitfall traps in each of the four selected habitats which were at least 60 m apart. Within each habitat type, 5 pitfall traps were set in an arranged 5 x 5 m square, with one in each corner and one in the centre. The traps (d = 7.5 cm, V = 200 mL) were partially filled with saturated sodium chloride solution. A drop of neutral-smelling detergent was added to reduce the surface tension of the solution. A Styrofoam roof was placed 7 cm above each trap to protect it from leaf litter and rainfall. Traps were sampled monthly during two growing seasons from May to December in 2008 and 2009.

All collected specimens were kept in 75% ethyl-alcohol with glycerol. Isopods were identified to the species level according to Frankenberger (1959); Vandel (1960, 1962); Schmöltzer (1965); Schmidt (1997) and nomenclature follows Schmalfuss (2003). All voucher specimens are deposited in the first author's collection at the Department of Biology, Faculty of Science, Zagreb.

2.3. Vegetation analysis

Vegetation of the fen and its surrounding habitats was sampled using phytosociological relevés according to the standard Central European methodology (Braun-Blanquet, 1964). We used the expanded cover-abundance scale (Barkman et al., 1964). Plant nomenclature follows Euro + Med PlantBase (2016). Terrestrial isopods, decomposers that feed mainly on dead plant material, prefer dicotyledonous over

monocotyledonous plant species (Rushton and Hasall, 1987). Thus, we calculated the ratio between dicotyledonous and monocotyledonous plant species based on phytosociological relevés to test if habitat preferences can be attributed to potential food sources. Nutrients were estimated indirectly by Ellenberg's indices, based on habitat preferences of plant species with regard to nutrient availability (Ellenberg, 1974; Ellenberg et al., 1992). Soil mineral nitrogen availability (N-index) ranges from 1 (for plant species growing on extremely nutrient-poor soils) to 9 (for nitrophilous plant species). We used the available data for each plant species' soil preference from Pignatti et al., (2005).

2.4. Soil analysis

In each of the four habitats, we took monthly measurements of soil temperature, soil moisture and pH during the two years of sampling. Soil temperature was measured at a depth of 7 cm using a P300 Dostmann electronic thermometer. We used soil cores (d = 10 cm, h = 2 cm) collected from each habitat to gravimetrically determine water content of the soil. Soil pH was measured in water with a ratio of 1:2.5 (10 g substrate/25 mL H_2O) using the WTW pH 330i meter.

2.5. Data analysis

One-way ANOVA or Kruskal-Wallis H test, followed by a Fisher LSD or a multiple comparison of mean ranks *post hoc* tests were applied to compare activity density of terrestrial isopods between the studied habitats. Prior to analysis, the data were tested for normality using the Shapiro Wilk W normality test. Seasonal dynamics were studied only in isopod species for which over 100 individuals were collected in the two years of sampling. Thus, we examined the seasonal activity of the four most abundant species, and the differences between habitats were tested with the same tests as total activity density. To study spatial and seasonal trends, we used pooled monthly catches of the two years, from May to December and present their mean values. Additionally, the Kruskal-Wallis H test, followed by a multiple comparison of mean ranks *post hoc* test, was used to compare Ellenberg's N-index and soil properties between the studied habitats. All tests were performed in Statistica 13.0 (Statistica, 2013).

To determine habitat preferences of isopod species in relation to the successional gradient, community data were analysed with the redundancy analysis (RDA) in the CANOCO version 5.04 package (ter Braak and Šmilauer, 2012). We used a linear model of ordination as the response data had a short gradient along the first axis (< 3 SD), as the recommended criterion for selecting between linear and unimodal models (Lepš and Šmilauer, 2003). Activity densities of all isopod species were used in the RDA, following log transformation. To test the significance of correlation between species occurrence and environmental variables (soil temperature, moisture and pH), a Monte Carlo permutation test using 499 permutations was performed.

Table 2
Terrestrial isopod species and their abundances recorded at the Jarak fen (Croatia) and surrounding sites during two consecutive years of sampling. Abundances are represented as total number of individuals (N) and frequency (%).

Species name	Fen		1st successional habitat		2nd successional habitat		Forest	
	N	%	N	%	N	%	N	%
Agnaridae Schmidt, 2003								
Protracheoniscus politus (C. Koch, 1841)	2	2.08	13	3.53	43	10.31	114	60.64
Armadillidiidae Brandt, 1833								
Armadillidium carniolense Verhoeff, 1901	4	4.17	40	10.87	59	14.15	2	1.06
Ligiidae Leach, 1814								
Ligidium germanicum Verhoeff, 1901	87	90.63	307	83.42	262	62.83	4	2.13
Trachelipodidae Strouhal, 1953								
Trachelipus rathkii (Brandt, 1833)	3	3.12	3	0.82	15	3.60	6	3.19
Trachelipus ratzeburgii (Brandt, 1883)			5	1.36	38	9.11	62	32.98
Species richness (S)	4		5		5		5	
Activity density (N)	96		368		417		188	

3. Results

3.1. Occurrence and activity density of terrestrial isopods

A total of 1069 individuals belonging to five species were collected in the fen and surrounding sites (Table 2). The most abundant species was *Ligidium germanicum*, accounting for 61.74% of the total catch. *Ligidium germanicum*, together with three other species: *Protracheoniscus politus* (16.09%), *Trachelipus ratzeburgii* (9.82%) and *Armadillidium carniolense* (9.82%), comprised over 97% of the total catch. Moreover, L. *germanicum* was highly abundant in the fen and both successional habitats (Table 2), while *P. politus* prevailed in the forest. Other species at the fen were rare and were recorded with maximum of four individuals in the two years of sampling.

Activity density of terrestrial isopods differed significantly between the four studied habitats (ANOVA, $F_{3,28} = 3.40$, $p < 0.001$, Fig. 2). According to Fisher LSD *post hoc* test, activity density was significantly higher in the 1st successional habitat ($p < 0.05$; range: 0–100, Fig. 2) and 2nd ($p < 0.001$; range: 14–110) compared to the fen. Terrestrial isopod activity density did not differ between the fen ($p > 0.05$; range: 0–28) and the forest ($p > 0.05$; range: 3–46) or any of the successional habitats and the forest ($p > 0.05$). We further examine the activity density of the four most abundant species.

There was a significant difference in the activity density of L. *germanicum* [Kruskal-Wallis H test, (3, N = 32) = 15.43, $p < 0.01$], *T.*

ratzeburgii [H (3, N = 32) = 14.07, $p < 0.01$], *P. politus* [H (3, N = 32) = 21.67, $p < 0.001$] and *A. carniolense* [H (3, N = 32) = 13.02, $p < 0.01$] between the studied habitats. The activity density of L. *germanicum* was significantly higher in the 1st (Fig. 3, mean ± SE, 38.38 ± 12.41) and 2nd successional habitats (32.75 ± 11.73) compared to the forest (0.5 ± 0.21, multiple comparison test, $p < 0.01$). However, there were no significant differences in the activity density between fen (10.88 ± 3.56) and both successional habitats ($p > 0.05$), or the fen and forest ($p > 0.05$). *Trachelipus ratzeburgii* was not recorded in the fen during the two years of sampling, thus its activity density was significantly higher in the forest (7.75 ± 2.27, $p < 0.001$) and 2nd successional habitat (4.75 ± 1.18, $p < 0.05$) compared to the fen. Differences in activity densities between other sites were not significant ($p > 0.05$). *Protracheoniscus politus* had significantly lower activity density in the fen (0.25 ± 0.71, $p < 0.001$) and 1st successional habitat (1.63 ± 0.80, $p < 0.01$) compared to the forest (14.25 ± 3.20). Additionally, there was significant difference in activity density between the fen and 2nd successional habitat (5.38 ± 1.28, $p < 0.05$), while differences between other sites were insignificant ($p > 0.05$). The activity density of *A. carniolense* was significantly higher in the 2nd successional habitat (7.36 ± 1.78, $p < 0.05$) compared to the forest (0.25 ± 0.16). The species activity decreased in the 1st successional habitat (5.00 ± 1.36) and fen (0.50 ± 0.37), but there were no significant differences in activity densities between other habitats ($p > 0.05$).

3.2. Seasonal dynamics of the dominant species

The most abundant species, *Ligidium germanicum*, had similar seasonal activity patterns across the sites, with the exception of the forest where the number of collected individuals was insufficient to determine seasonal activity (Fig. 3). The maximum seasonal activity of L. *germanicum* was observed in June, while the number of individuals decreased during the summer, and no individuals were collected in December at the fen or at the 1st successional habitat. Seasonal activity of *Protracheoniscus politus* was expressed exclusively in the forest, with maximum seasonal activity observed in August. The two other dominant species, *T. ratzeburgii* and *A. carniolense*, did not show strong seasonal peaks in activity density.

3.3. Terrestrial isopod assemblages and environmental variables

Environmental variables explained 54.7% of the total variation in terrestrial isopod assemblages in redundancy analysis. The eigenvalues of the ordination axes were 0.329, 0.209, 0.009 and 0.178, respectively. A Monte Carlo randomization test showed that the ordination was statistically significant (F = 13.7, p = 0.002). Along the first ordination axis, most of the fen and both successional habitats were positioned to
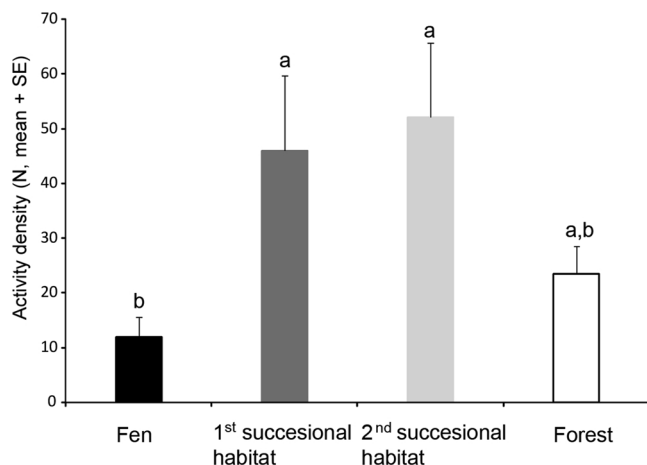

Fig. 2. Terrestrial isopod activity density in the Jarak fen and surrounding sites (mean + SE). Letters indicate a significant difference between habitats (*1-way* ANOVA, Fisher LSD *post-hoc* test, $p < 0.001$). Activity density (N) is represented by mean number of individuals recorded during two consecutive years of sampling.
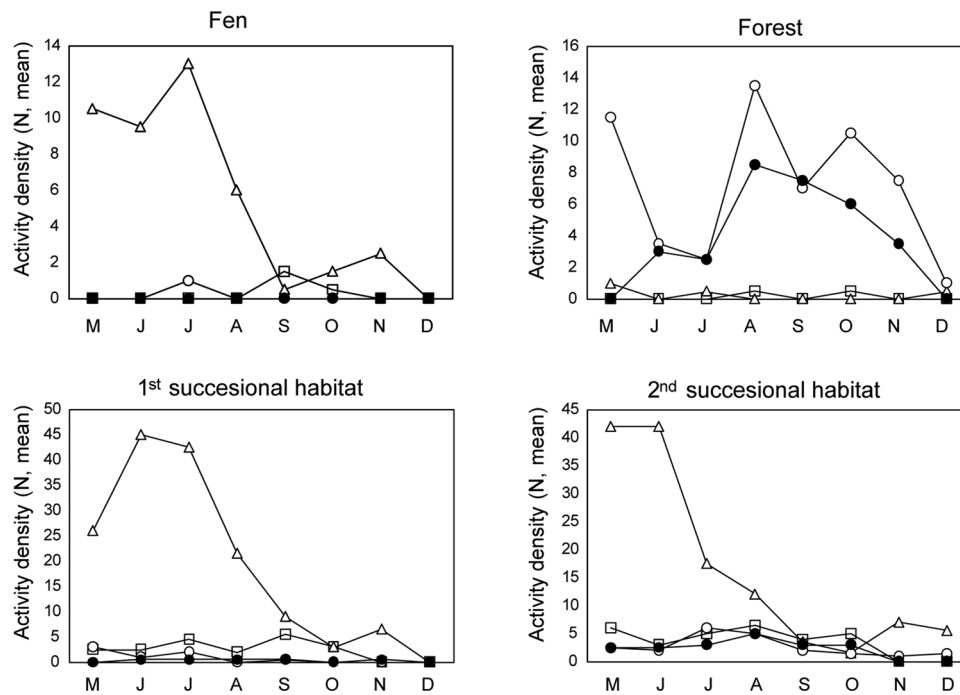
Fig. 3. Seasonal activity of four dominant terrestrial isopod species at the Jarak fen (Croatia), succession habitats and forest. Monthly mean was calculated based on two consecutive years of sampling for each species: *Armadillidium carniolense* (□), *Ligidium germanicum* (Δ), *Protracheoniscus politus* (○) and *Trachelipus ratzeburgii* (●).
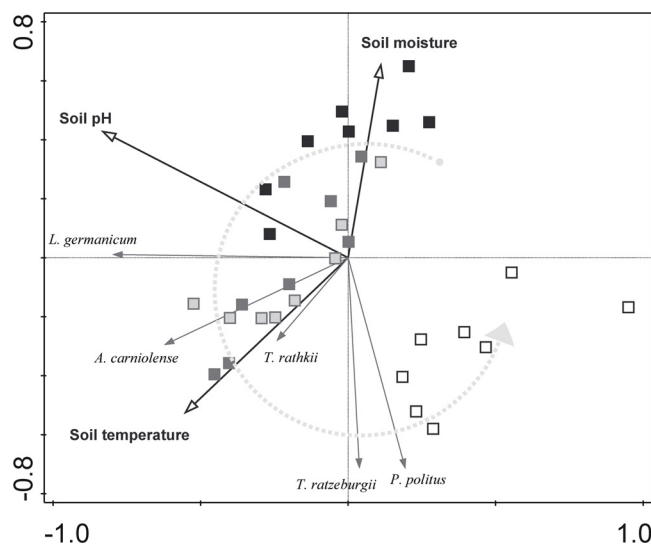

Fig. 4. RDA ordination of terrestrial isopods and environmental variables across four studied habitats indicated with the squares: fen (black), 1st successional habitat (dark grey), 2nd successional habitat (light grey), forest (white). Environmental variables are shown with black arrows. Arrow lengths represent the relative importance of the explanatory variables and their directions indicate positive or negative correlations. Dashed line follows hypothetical ecological gradient from the fen to the forest.

the left of zero, while forest habitats were positioned to the right (Fig. 4). Fen sites are related to the upper part of the second axis, while successional habitats are related to the lower part of the second axis. Habitat position in the ordination, with fen and forest sites at the two extremes and with the overlapping 1st and 2nd successional habitats placed in between, suggests ecological succession. Thus, it is possible to interpret both axes as the axes of a hypothetical ecological successional gradient. Along this gradient, terrestrial isopod community clearly changes. *Ligidium germanicum* was highly abundant in the fen and successional habitats and its occurrence was positively associated with

high soil moisture and pH. On the contrary, *P. politus* and *T. ratzeburgii* were extremely rare at these sites, and were negatively associated with higher soil moisture and higher pH values (Fig. 4).

This pattern was mainly governed by soil properties, specifically soil moisture, which decreased along the successional gradient, starting from fen sites to successional habitats. Fen soil was saturated with water during the growing seasons, with surface water regularly present, and soil moisture differed significantly from the three other studied habitats (Table 1). Additionally, successional habitats are positively related to higher soil pH values and soil temperatures. The mildly alkaline soil of both successional habitats was also characterised by higher soil mineral nitrogen availability compared to the fen soil (Table 1). Additionally, in these habitats dicotyledonous plants were almost five times as numerous than monocotyledonous plants, suggesting that successional habitats provide a greater amount of the best quality food for terrestrial isopods. Plant species richness increases along the successional gradient, from the fen to the 2nd successional habitat, though it decreases in the forest, implying higher structural complexity of successional habitats. The fen soil was nutrient poor, with dicotyledonous plants almost twice as common as monocotyledons, though the latter prevailed in abundance.

4. Discussion

4.1. Spatial changes of terrestrial isopod assemblages

This study revealed an increase in activity density of terrestrial isopods along a successional gradient from the fen towards the 2nd successional habitat. This pattern was caused by physical and chemical soil properties and vegetation structural complexity. High water saturation of the fen, with a mean soil moisture over 80% during the growing season, and sparse vegetation without a well-developed root-system likely caused unfavourable conditions for terrestrial isopods, as it would reduce suitable shelter sites and food availability. This corresponds well with previous findings that hydrological conditions associated with flooding affect terrestrial isopods communities by decreasing their species richness and population density (Plum, 2005).

Additionally, our previous studies showed that terrestrial isopods maintain stable populations in acidophilous peatlands, particularly in *Sphagnum* dominated sites overgrown with *M. caerulea* grass, while in permanently semiaquatic microhabitats their density is strongly decreased (Antonović et al., 2012; Brigić et al., 2017b). Overall, the fen isopod community was species-poor and characterised by low population density. Most of the collected species, with the exception of L. *germanicum*, were not present in the fen habitat suggesting that most species cannot tolerate such extreme conditions. Thus, our findings suggest that groundwater level at the studied fen is still sufficiently high to suppress invasion of forest terrestrial isopod species into the fen.

Successional changes, as seen by the spread of *Salix*, *Populus* and *Petasites* plants, lowered the water table level and supported formation of a litter layer in successional habitats. Furthermore, these successional habitats contain a more species rich and diverse plant community compared to the fen (Bujan et al., 2015). The variety of microhabitats and food sources, such as litter, favour establishment of a highly diverse soil community (Lavelle and Spain, 2001), including litter-breaking macrofauna. Similar patterns of increased density were documented for soil decomposer macrofauna in post-mining chronosequences with increasing succession age (Frouz et al., 2001) and in succession habitats of the studied fen for other soil dwelling animals, e.g. ants (Bujan et al., 2015). Thus, the favourable microclimatic conditions and higher nutrient availability at the successional habitats supported colonization of three forest dwelling isopods: *P. politus*, *T. ratzeburgii* and *A. carniolense* in addition to L. *germanicum*.

Furthermore, the vegetation composition of successional habitats, in particular the spread of the dicotyledonous plant *Petasites hybridus,* is important for two reasons. First, its broad leaves create dense stands that provide shade and ensure safe movement of isopods during hot summer months by reducing desiccation to which terrestrial isopods are sensitive (Sutton, 1972). Similarly, Hornung (1990) documented the aggregation of terrestrial isopods within dense vegetation stands. Additionally, such aggregation could be enhanced by the occurrence of dicotyledonous plants, a favourite food resource for terrestrial isopods (Rushton and Hasall, 1987), which were almost five times more abundant at the successional habitats compared to the fen. Furthermore, successional habitats were more nutrient rich than the fen.

4.2. Habitat preferences of terrestrial isopods

Among the four dominant species, we found a clear habitat preference as documented by species activity density and RDA analysis. *Ligidium germanicum* was most abundant in the successional habitats and the fen, as this species inhabits moist habitats and can tolerate high water table levels (Antonović et al., 2012; Tomescu et al., 2015). Permanent populations of L. *germanicum* have been recorded in acidophilic peatlands (Ternjej et al., 2015; Tomescu et al., 2015; Brigić et al., 2017b) and semi-natural fens (Sterzyńska et al., 2015b). During winter months, when temperatures drop below freezing, isopods migrate to deeper soil layers to survive (Sutton, 1972; Warburg et al., 1984). However, because the fen soil was permanently saturated with water, it remains unclear how L. *germanicum* survives the extreme winter temperatures in this moist environment. The wintering strategy of this species should be elucidated in future research.

Other species were rarely recorded in the fen, e.g. *P. politus* and *A. carniolense*, and no evidence was found indicating the presence of stable populations. *Protracheoniscus politus* is a dominant forest species (Štrichelová and Tuf, 2012) occurring in areas with deep leaf litter (Radu and Tomescu, 1976; Warburg et al., 1984), and therefore, its abundance in the forest and successional habitats was expected. *Armadillidium carniolense*, a forest species (Tomescu et al., 2002), was abundant in both successional habitats, where microhabitats were clearly favoured. Another forest species, *T. ratzeburgii* (Štrichelová and Tuf, 2012) was completely absent from the fen, suggesting that *T. ratzeburgii* avoids areas of high soil moisture and low vegetation density.

Similarly, our previous studies showed that this forest trio rarely entered acidophilic peatlands, but were abundant at their edges and in the adjacent forests (Antonović et al., 2012; Brigić et al., 2017b). Additionally, *T. ratzeburgii* shelters beneath trunks, decaying branches or litter, thus its activity in successional habitats could be underestimated using the pitfall traps.

4.3. Temporal changes in the activity of dominant species

We found that the seasonal activity of L. *germanicum* was most pronounced in spring and early summer, with a maximum observed in June. This activity pattern corresponds to the activity of both sexes, with a one-month separation between the peak activity of males and females. Early in the season, males search for receptive females, while female activity peaks later in the season when they search for optimal shelter sites for brood development (Dangerfield and Hassall, 1994). In this study, the seasonal activity of L. *germanicum* peaked one month later than in beech forests and mixed beech and spruce forests in Romania (Ferenti and Covaciu-Marcov, 2012). Terrestrial isopod species exhibit different temporal dynamics, which is largely dependent on their breeding strategies and climatic condition of the area (Hornung, 1990; Dangerfield and Hassall, 1994; Zimmer and Brauckmann, 1997). Thus, these differences in seasonal dynamics of our dominant species between the literature and our results could be due to the elevation of our studied fen (690 m) and colder winters with lower temperatures in this region. The montane altitude can act as a strong environmental filter in shaping terrestrial isopod communities of fens and surrounding habitats (Sterzyńska et al., 2015a).

In conclusion, successional changes have a positive effect on activity density and richness of terrestrial isopods, enabling the persistence of stable populations of terrestrial isopods and colonization of forest species. In contrast, fen isopod community was species poor and characterised by low population density. This implies that the groundwater level at the fen is high enough to suppress the invasion of forest species into the fen. However, the lack of peatland management practices will certainly lead to changes in the composition and structure of terrestrial isopod community in the fen. Additionally, seasonal activity of terrestrial isopods begins in late spring, however this is expected to change with the global increase in temperature and phenological changes. These changes will ultimately cause a loss of peatland specialized plant and animal species, which could have detrimental effects on biodiversity. This study provides insight into the spatial and temporal changes in common terrestrial isopods and their phenology, which could provide predictions about future impacts on this taxon in a changing climate.

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